

THE THORACIC AND CERVICAL SCLERITES OF INSECTS.

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CONTENTS.

	PAGE
I. Introduction.....	35
II. Historical Review.....	37
III. Discussion of Thoracic Sclerites.....	48
1. Tergum.....	48
2. Wings.....	50
3. Pleuron.....	51
4. Epimeron.....	55
5. Episternum.....	58
6. Precoxale.....	62
7. Trochantin.....	65
8. Coxa.....	67
9. Sternum.....	69
10. Intersegmentalia.....	73
11. Cervical Sclerites.....	74
IV. Summary.....	78
V. Bibliography.....	79
VI. Terminology.....	82
VII. Explanation of Plates.....	83

INTRODUCTION.

This paper is presented as the morphological part of a thesis for the degree of Doctor of Philosophy at the Massachusetts Agricultural College. It has been prepared under the supervision of Dr. H. T. Fernald and Dr. G. C. Crampton, to both of whom I wish to express my sincere thanks for the many ways in which they have guided and helped me in the work. I am also indebted to Dr. G. C. Crampton who has kindly furnished all the material upon which this paper is based and by which it was made possible.

Some of the literature used and referred to was obtained from the library of the Massachusetts Agricultural College. Other volumes were obtained from the Boston Society of Natural History, through Dr. H. T. Fernald. Most of the books, however, were loaned from the private libraries of Dr. C. H. Fernald, Dr. H. T. Fernald, and Dr. G. C. Crampton, to each of whom I am greatly indebted for their use.

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The homologies of the thoracic sclerites have been greatly confused, owing to the fact that most investigators have given their own views, without first giving sufficient study to the work and terminology of previous writers. This has resulted in the invention of new terms and the misapplication of those already in use. Both the old and new terms have often been applied to identical sclerites and consequently the terminology is also in a chaotic condition.

Some of the more recent writers have attempted to show the unity of thoracic structure, which exists in all insects and to introduce a terminology which will be as uniform as possible. This is a very difficult task to accomplish because of the great confusion which exists.

In this paper an attempt is made to help straighten out the homologies and terminology of the thoracic sclerites of insects. An effort has been made as far as possible, to use the terminology most widely accepted and which has the right of priority. Where recent terms have been applied to sclerites, for which the old terms seem inadequate or undesirable, the new terms have been adopted. In some cases entirely new terms have been applied to sclerites, but only where the condition of the terminology seemed to warrant such action and where, in the opinion of the writer, an improvement could be made.

Especial attention has been given to a study of the pleuron and sternum. The tergum and wings have not been investigated so thoroughly and consequently a discussion of these parts is not given in detail. All the specimens were studied under a liquid medium (water, alcohol or glycerine), with the aid of a Zeiss binocular microscope. A bull's eye condenser was used to concentrate the rays of an electric light upon the object under study. In many cases the specimens were first boiled in 10% potassium hydroxide. The internal tissues were then washed out with running water, thereby making the sclerites show up clearly and leaving the internal processes intact. This procedure greatly facilitated the determination of the thoracic sclerites and their sutures.

HISTORICAL REVIEW.

Several theories have been proposed to explain the probable formation of the thoracic segments and almost every writer seems to have a different view of the subject. This has led to the formulation of many different theories, some of which are merely the unsupported statements of their respective authors, who have failed to give reasons for their views. Such theories apparently have no evidence to support their presentation and hence cannot be accepted, especially when other writers have advanced differing theories established upon firmer grounds. Some investigators have based their ideas of the thorax upon the study of a limited number of insects, whereas they should have studied at least a representative number from different groups, in order to obtain a general conception of the thorax. Others who have studied a large number of insects have failed to recognize the relation that exists between the thoracic sclerites. This has given rise to incorrect interpretations of the formation of the thorax and to great confusion in the homologies of the thoracic sclerites in the same and in different insects.

The earlier entomologists wrote very little about the insect thorax. Knoch, 1801, termed the prothorax "Collum" and the meso-, and metathorax, "Pectus." He may have recognized that the thorax was composed of three segments, which are topographically grouped into two parts, the collum and pectus, or he may have considered that the thorax was actually composed of only two segments, viz.: the collum and pectus.

Chabrier, '20, Kirby, '28, and later Verhoeff, '02-'04, although aware that the thorax was composed of at least three segments, thought that it might be divided according to function into two parts. These two parts were termed by Chabrier, the collier and tronc alifere; by Kirby, the manitruncus and alitruncus; and by Verhoeff, the proterothorax and deuterothorax. This idea is no longer accepted.

Audouin, '24, upon whose investigations the modern conception of the thorax is based, points out that it is composed of three simple segments and was the first to work out a terminology for the thoracic sclerites, which has been used by all subsequent entomologists. Beginning with the anterior thoracic segment, he named them the pro-, meso-, and metathorax,

terms which seem to have been first used by Nitzsch, '18, although Nitzsch called the first segment the protothorax instead of prothorax. Audouin regarded each thoracic segment as made up of four parts; a dorsal region, the tergum; a ventral region, the sternum; and two lateral regions, the pleuræ. He thought that the tergum was composed of four transverse subdivisions, lying one behind the other in consecutive order. Beginning with the anterior one, he termed these the prescutum, scutum, scutellum and postscutellum. The sternum he regarded as a single piece. For each lateral region or pleura he described and named several pieces, viz.: two large lateral sclerites, the anterior one termed the episternum and the posterior one the epimeron; a small narrow piece lying along the anterior edge of the episternum termed "paraptere," (previously called "hypotere" by Audouin, '20); a small sclerite containing the spiracle termed the peritrema and a sclerite articulating with the epimeron termed the trochantin.

Audouin was mistaken in his definition of the last mentioned sclerite, because the trochantin articulates with the episternum, not with the epimeron. Later Audouin, '32, defined the "paraptere" as "the small piece so visible in Hymenoptera and Lepidoptera, which covers the base of the fore wings and which is variously designated by the terms *ecaille*, *epaulette* or *squamula*." (Audouin's trans. of Mac Leay's paper, "The comparative anatomy of the thorax in winged insects, following a review of the actual state of the Nomenclature." pp. 41, footnote by Audouin). According to this statement the "paraptere" is evidently synonymous with *tegula*.

Subsequent entomologists in applying this terminology for the thoracic sclerites have misinterpreted the homologies and consequently confused the names. Several sclerites, which Audouin apparently failed to recognize, have since been described. In descriptions of these, different investigators have invented new terms for identical sclerites, leading to more confusion.

In all insects there is a common ground plan, which is more modified in some, less so in others. On this basis recent writers have attempted to work out a uniform system of terminology applicable to all insects. In order to do this, it is first necessary to correctly homologize the sclerites in the

different orders of insects and then to straighten out the confused terminology which has been applied to them—an almost impossible task.

Straus-Durckheim, '28, believed that the thorax was composed of three segments and suggested that the cervical sclerites represent the remains of two segments, situated originally between the head and prothorax. This suggestion will be discussed under the heading, Cervical Sclerites.

Mac Leay, '30, considered that each thoracic segment was made up of four subsegments or annuli, represented in the tergum by the prescutum, scutum, scutellum and postscutellum. In the *Zoological Jour.* 1830, Vol. 5, pp. 160, he states that "owing to the development of the tergum, the pectus in Hymenoptera is exceedingly diminished. But were each of the sternums at its maximum of development, it would also be found to consist of four pieces like a tergum. This is the case in Julidae and is more or less apparent in Annulosa. For instance, the pectus of the prothorax in *Squilla* has a praesternum, sternum, sternellum and poststernum." Mac Leay leaves the pleuron out of consideration. According to modern ideas his view of the tergum is erroneous, since the tergum is made up of but two plates, as Verhoeff, '02, Snodgrass, '09, and others have proved. The anterior of these two plates is subdivided into regions by sutures, these regions being termed the prescutum, scutum and scutellum. The posterior plate is termed the postscutellum. Since Mac Leay claims that the four sternal plates described by him occur in the pectus of the Julidae, which are diplopods, and in *Squilla*, which is a crustacean, his theory is not at all necessarily applicable to insects.

Newport, '39, evidently agreed with Mac Leay regarding the formation of the thoracic segments. He thought that each was made up of four subsegments or annuli, represented in the tergum by the prescutum, scutum, scutellum and postscutellum. These annuli, he thinks are partly fused in the pleural region and completely fused in the sternal region. Newport added nothing new to this theory of Mac Leay's and it must be regarded as untenable. Newport, however, brought forth a new view pertaining to the cervical sclerites, which will be referred to later. Furthermore, he is incorrect in his statement that Audouin considered each thoracic segment to be

composed of four subsegments, for, as already stated, Audouin appears to have believed that the thorax consisted of three simple segments.

Schiodte, '56 and Winslow, '62, followed Audouin's ideas and believed that the thorax was composed of but three segments, the pro-, meso-, and metathorax.

Packard, '80, seems to have regarded the thorax as made up of three simple segments, but his interpretations and methods of homologizing the thoracic sclerites in the insects of the different orders which he studied, are incorrect. The homologies of the thoracic sclerites will be discussed further on.

Miall and Denny, '86, in their book on the Cockroach, considered that the thorax was composed of three segments and suggested that the chitinous plates at the base of each leg in the roach (i. e. epimeron, episternum, trochantin, etc.) represent "two basal leg joints, which have become adherent to the thorax," although in other cases they state that they belong "to the thorax and not to the leg."

If these sclerites at the base of the leg in the roach represent leg "joints," there would probably be more definite traces of these joints in other insects, especially as the leg is such an important appendage. In the embryo of the cockroach the coxa is apparently the only basal leg segment present and there are no indications of other leg segments which have or which might become adherent to the thorax. This is true for other insects as well as for larvae and primitive forms. Moreover, it is improbable that such leg segments, if present, would form the lateral wall of the segment or pleuron which Miall and Denny thought was the case in the Mole Cricket. It seems more probable that the basal leg "joints" or segments would remain in place and not move up into the pleural region. Börner considered the pleural plates as part of the sternum, but later with Hennequy, thought that they were plates of the basal leg segments.

Hagen, '89, advanced the theory that each thoracic segment was composed of three subsegments, each subsegment bearing a characteristic appendage. The anterior he terms the leg bearing, the next following the wing bearing, and the posterior, the spiracle bearing subsegment. Some of the subsegments develop more than others. On the prothorax of Strepsiptera and agrionids, he finds traces of "wings."

The spiracle does not occur in all the thoracic segments, being absent in some cases. Whether the spiracles which often occur between the thoracic segments belong to the immediate anterior or to the immediate posterior segment, is uncertain and at present a disputed question. What Hagen considered rudiments of wings on the prothorax of Strepsiptera and agrionids, have proved to be merely flaps and are no longer considered homologous with wings. Several fossil Palaeodictyoptera have a pair of lateral wing-like appendages on the prothorax, like rudimentary organs, but it is very uncertain whether these appendages do or do not represent traces of wings.

Patten, '90, claims that each thoracic segment is composed of two annuli. Using the nervous system of *Scolopendra* as a type, he found in all arthropods studied, two cross commissures in each neuromere, thus indicating the double nature of these structures. In *Acilius* the median furrow between the cross commissures was similar to that found between the successive neuromeres. In *Scorpio*, the neuromeres are distinctly double and in such forms as *Julus*, the cardiac ostia, arteries, tracheæ and legs show the double nature of the somites. Segmental fusion is also indicated by two pairs of tracheal invaginations in each segment of *Acilius*, by the bifurcated appendages of many crustacea and by the bifid maxillæ of insects, the latter group frequently having monsters with double pairs of legs.

Patten's double segment theory based upon the reasons cited above, does not coincide with the facts in all cases, and hence is open to objections. Furthermore, what occurs in *Scolopendra* should not be given too much weight, when considering the condition found in insects. In insects the last abdominal segment is considered as the fusion product of several neuromeres and yet it contains only two cross commissures, whereas according to Patten's idea, there should be as many commissures present as neuromeres. In Vermes the neuromeres of each segment contain but two cross commissures, although the segments are not double. The median furrow between the cross commissures in *Acilius*, if there is a furrow, which is doubtful, can hardly be similar to that between the successive neuromeres, for the latter are separated by a considerable distance. In such forms as *Julus*, Patten found the double nature

of the somites indicated by the cardica ostia, arteries, tracheæ and legs, but this does not prove the double nature of the somites in insects. Embryologists in general, seem to have never found two pairs of tracheal invaginations in any one segment in insects. Patten's second pair of tracheal invaginations in *Acilius* has proved to be a mass of cells, easily mistaken for tracheal invaginations. Monsters with double appendages occur throughout the animal kingdom very frequently and are generally considered as abnormalities; not as a reversion to primitive types or conditions.

Lowne, '90, favors the compound segment theory of Patten, but thinks that it has not been sufficiently proved.

Banks, '93, in studying the chilopods observed a coalescence of the thoracic segments, less apparent in the lower forms (*Geophilus*) than in the higher ones (*Scutigera*) and from this concluded that the thorax of insects is composed of five segments, the first, third and fifth bearing legs, the second and fourth bearing wings. He points out in support of this theory that *Machilis* has a pair of small rudimentary appendages on each abdominal segment, which are also found on the meso- and metathorax in addition to the legs. From this, he argues, that the rudimentary appendages represent legs and hence, that the meso- and metathorax are compound segments.

These rudimentary appendages found in *Machilis* occur in other insects, also in Myriopoda and are the so-called styli—not vestigial legs. Jourdain, '88, considered these styli as homologous with the exopodite of Crustacea. Haase, '89, regarded them as modified setæ. Henneguy, '04, homologizes the styli with the epipodite of the crustacean leg and Verhoeff, '04, compares them to the coxal organs of Myriopoda. At present, however, it is not known exactly what the styli are, but they certainly are not regarded as vestigial legs by modern investigators. Banks' theory has no embryological support and furthermore, what occurs in chilopods is not necessarily any criterion of what occurs in insects.

Kolbe, '93, considers that the thorax is composed of three primary segments between which, he finds marked off, other "complementary segments," in such forms as the larvæ of *Lampyrus* and *Raphidia*, also in *Locusta*, *Oedipoda*, etc. His conclusions are based principally on the larvæ of *Lampyrus* and

Raphidia and he was the first to suggest the possibility of the occurrence of intersegmental or "complementary segments." This is not supported by embryology, however, which gives no indication of "complementary segments." Larvæ frequently acquire secondary adaptative structures, which cannot be considered as a retention of the primitive condition and the "complementary segments" of the above mentioned larvæ are probably some such secondarily acquired structures. Kolbe's theory needs more proof to support it than the presence of secondarily marked off regions in larvæ. A dissection of the larva of a beetle in which there are present "complementary segments" identical with those described by Kolbe in the larva of *Lampyrus* demonstrates the following facts: that the "complementary segments" have no segmental muscles or other segmental structures; that the "complementary segment" is apparently a fold of the sternal integument and does not extend to the tergum; that it belongs to the segment in front of it and that each actual segment is marked off by an internal ridge, which extends completely around the body and has longitudinal segmental muscles connecting one ridge with the next. These three ridges probably define the three thoracic segments.

Walton, '00, is the exponent of another double subsegment theory which is similar to Banks'. He considers the coxa in the Hexapoda and Chilopoda as the fusion product of the appendages of two primary metameres which he terms, "coxa genuina" and "meron." The meron represents the rudimentary appendage of the posterior metamere, which articulates with the epimeron, and the "coxa genuina" represents the basal leg segment of the functional appendage of the anterior metamere, which articulates with the episternum and has persisted. From this he concludes that each segment is composed of two metameres. Walton's idea that the meron represents a vestigial leg is as improbable as Banks' view, that the styli of *Machilis* were the vestiges of legs. There is no embryological evidence to support Walton's theory and he has since repudiated it.

Comstock and Kochi, '02, think each thoracic segment is composed of two subsegments, which have become fused together. The line of division between them is represented in the tergum by the suture between the scutum and scutellum, in the pleuron by the pleural suture and in the sternum by the furcæ.

This theory is open to the same objections as the other compound segment theories previously stated, viz.: that embryology gives no indications of compound thoracic segments. Primitively the episternum and epimeron appear to consist of a single plate, a portion of which has become drawn inward, probably by muscular stress, forming a hollow infolding of the integument, which is represented externally by the pleural suture and internally by the lateral apodeme. The anterior sclerite formed by this infolding of the pleuron, is termed the episternum, and the posterior sclerite, the epimeron. If this explanation be true, Comstock's and Kochi's view, as well as Banks' and Walton's idea which is very similar, namely, that the pleural suture is the line of union between two subsegments, must be regarded as untenable.

Verhoeff, '02-'04, made an extensive study of the comparative morphology of the insect thorax and his conclusions are based mainly on the thorax of the Chilopoda, Apterygota, Orthoptera, Dermaptera and Embiidæ. His theory is an elaboration of the views advanced by Kolbe. In studying *Japyx*, Verhoeff found in front of the "chief segments," represented by the pro-, meso-, and metathorax, indications of three other segments, which he called complementary segments and termed them micro-, steno-, and cryptothorax respectively. Thus the thorax would consist of six primary segments viz., micro-, pro-, steno-, meso-, crypto-, and metathorax. He found, on further study, that in front of each of these six primary segments were a few small sclerites, which he considered as the remains of six other segments and termed them the intercalary segments. Hence according to Verhoeff the thorax would consist of six primary and six intercalary segments, making a total of twelve thoracic segments, or in other words, each segment of the thorax consists of four annuli. This theory has been severely criticized by several writers and now is generally considered as incorrect. Silvestri, '02, and Börner, '03, criticized Verhoeff's views and the latter shows by his figures that Verhoeff's statements are erroneous. Börner states that the thorax is composed of three segments with intersegmental regions.

Voss, '04, gives Kolbe's and Verhoeff's composite segment theory, stating four possible modifications of it, which can be

found in diplopods, *Scolopendra*, *Geophilus* and *Scolopendrella*. He thinks that the pre-segmental chitinous plates in insects are a secondary differentiation, explainable by mechanical causes as represented in lampyrid larvae.

Enderlein, '07, regarded the complementary segments in *Japyx*, which correspond to Verhoeff's micro-, steno-, and cryptothorax as "constricted-off" portions of the pro-, meso-, and metathorax and terms them the apotom of their respective segments. That is to say, they are detached portions of the pro-, meso-, and metathorax.

Desguin, '08, attacks Verhoeff's theory and shows that embryology, anatomy, musculature, etc., give no evidence in support of it. Other writers have criticized Verhoeff's ideas and it has been shown that all the facts seems to be contrary to his views. Unless further evidence is brought forth to substantiate Verhoeff's theory of the composition of the insect thorax it must be regarded as untenable.

Henneguy, '04, reverts to Kolbe's theory and expresses similar ideas. He finds in the larva of *Lampyris*, that each tergum covers two ventral "segments," the first of which bears a pair of spiracles and is known as the complementary segment, while the second segment bears a pair of legs. He finds these same conditions in *Scolopendrella* and from this concludes, first, that the Myriopoda are ancestors of insects; second, that the present position occupied by the spiracles in adult insects is explainable on the ground, that they are borne on the complementary segments. Henneguy finds traces of complementary segments in the thoracic region of elaterid and staphylinid larvae and in the abdominal region of carabid larvae. He finds that in the larva of *Raphidia*, the complementary segment between the pro-, and mesothorax, is a complete segment. The larvae of some Diptera appear to have double the number of segments present in other larvae of the same family, each complementary segment being produced by a transverse constriction of such a nature, that a sort of intermediate segment is formed between the normal segments. Henneguy states, that according to Brauer, this arrangement is due to a lengthening of the membrane uniting two consecutive segments, or to a secondary constriction of each annulus.

What has been said of Kolbe's theory will also apply to Henneguy's views. Henneguy's conclusions that Myriopoda are the ancestors of insects and that the position of the spiracle is to be explained by supposing that they were borne by the hypothetical complementary segment must have a firmer foundation before they can be accepted. Whether the spiracles belong to the segment in front of them or to the segment behind them is at present a disputed question. The spiracles are usually absent in the prothorax. It certainly seems more probable that the so-called complementary segments are parts of the pro-, meso-, and metathoracic segments, since this view is supported by embryology, anatomy, musculature, etc.

Woodworth, '06, states that "theories of composite segments in the thorax seem to be entirely untenable." He appears to consider the thoracic segment as originally made up of a solid ring, which later becomes split in the following manner. The development of the legs, results in the separation of the sternum from the remainder of the segment; in the beginning of the formation of the pleural suture; and of the suture which ultimately separates the scutum from the scutellum. The development of the wings results in the completion of the above mentioned sutures; in the development of the prescutum and postscutellum, and in the separation of the tergum from the pleuron. Hence he concludes that the wings are not the product of the pleuron or the notum, but are the means of their differentiation phylogenetically and ontogenetically.

Woodworth's conception of the thoracic segment is no longer accepted by most entomologists, although many originally held the same view. In all primitive insects and in larvae the sclerites arise as numerous islands of thickened chitin and not as a solid chitinous ring, which later becomes split up. In the more specialized insects these small sclerites become more or less fused together. This can be clearly demonstrated by studying a series of insects beginning with larval and primitive forms as *Eosentomon*, and gradually working up to the more specialized groups.

Berlese, '06, regarded each thoracic segment as originally made up of a "tergite" and "sternite." The "tergite" was one solid piece which included the "alar sclerites," the spiracles, the tergum and the epimeron. The "sternite" is composed of

four pieces which he termed the acro-, pro-, meso-, and metasternites. The acro and prosternites constitute the "sternum," while the meso- and metasternites form the "sternellum." With this as a basis Berlese accounts for the sclerites which make up a typical thoracic segment in the following manner. First, the epimeron became split off from the "tergite," while the leg appendage arose from a part of the "metasternite" and later the trochantin, consisting of two pieces became split off from the "sternellum," in the region of the coxa. Next, the epimeron entered into the composition of the pleuron near the coxa and the two "alar plates" at the base of the wings, together with the spiracles, became detached from the "tergite." The "sternum" became split up into pieces to form the episternum and sternum. It is obvious that Berlese's theory is untenable. Considered from an embryological and anatomical point of view, it has no foundation whatever.

The later writers, Crampton, '08-'09 and Snodgrass, '09-'10, think that the thorax of insects is composed of three segments. This view is supported by embryology and anatomy and is based upon facts, while all the composite segment theories are more or less lacking in such support, are not always based upon facts and consequently are untenable.

Dr. Prell, '13, who has recently published a paper on the Myrientomata, views the insect thorax as follows: In the abdomen of *Acerentomon*, he finds that each segment is divided into four rings, which are further subdivided into regions by sutures. In the thorax of *Eosentomon* these rings are represented by a number of sclerites which have become more or less displaced from the ring arrangement, owing to the specialization of the thorax for locomotion. The sternal region is composed of four subdivisions, which he terms the acro-, pro-, meso-, and metasternite. The tergal region is also composed of four subdivisions, the acro-, pro-, meso-, and metatergite and in addition a region called the nototergite becomes secondarily marked off from the metatergite. In the pleural region of each segment, he finds two longitudinal rows of sclerites. Those bordering on and extending along the lateral margin of each thoracic sternum, he terms the sternopleura or pleura in the restricted sense. Those which border on and extend along the lateral margin of each tergal region, he terms the sympleura or tergal pleura. Both sympleura and pleura are composed of four sclerites, lying one

behind the other. The dorsally situated sympleura are termed, acro-, pro-, meso-, and meta-sympleurites, while the sclerites composing the more ventrally situated row are termed the acro-, pro-, meso-, and meta-pleurites. The pleura and sympleura, he thinks, are detached portions of the region, which he terms the zygoterga. The zygoterga is the region comparable to the dorsal or tergal half of the abdominal segment. Thus he considers that each thoracic segment is composed of four sub-segments designated by the terms acro-, pro-, meso-, and meta-subsegments, that the dorsum is composed of four tergites and the sternum of four sternites, designated by the above mentioned prefixes. He regards the lateral region as consisting of two longitudinal rows of sclerites (i. e., the upper row or sympleura and the lower row or pleura) and considers that they are detached portions of the zygoterga.

DISCUSSION OF THE THORACIC SCLERITES.

TERGUM. The term dorsum has been used to designate various parts of the dorsal surface of the thorax in different insects, but when correctly applied it refers to the entire dorsal surface and this usage will be followed here. The terms tergum and notum will be used interchangeably to designate the entire dorsal surface of any one thoracic segment. These terms are generally used in this sense and if given any other meaning, would lead to confusion.

In the nymphs of the lower insects as well as in many larvæ and pupæ, the tergum is a single undivided plate, the scuto-scutellum (Crampton, '09). This is probably the primitive condition of the tergum, which has possibly persisted in a more or less modified condition in the pronotum of adult insects. The fact that no postscutellum has ever been described as occurring in the pronotum of insects, supports this view. The post-scutellum in adult insects, develops in the intersegmental membrane of the mesonotum and metanotum, its development being apparently parallel with the development of the wings, which is possibly due to anatomical causes such as the stimulus of muscle stress, etc. Snodgrass, '10, calls the postscutellum the "postnotum" or "pseudonotum." There is no reason for rejecting Audouin's term postscutellum, which is suitable, widely used and generally accepted. Hence it will be retained in this paper.

Verhoeff, '02-'04, Voss, '04, and Snodgrass, '09, have proven conclusively that the tergum is composed of but two plates, the scutoscutellum (Crampton, '09) and the postscutellum (Audouin, '24), the latter being absent in the pronotum, (Fig. 13, scsl, psl). The anterior plate or scutoscutellum is generally marked off by transverse sutures into three regions, the prescutum, scutum and scutellum, but sometimes the sutures which mark the boundaries of these regions are absent (Fig. 13, prsc, sc, sl). In many insects the posterior plate or postscutellum is divided longitudinally into a median and two lateral regions, which may be subdivided (Fig. 1, psl). Crampton, '09, termed these regions the mediophragmite or median region and pleurophragmites or lateral regions. I shall use the terms mediotergite and pleurotergite for these regions, because they are subdivisions of the tergum (Fig. 1, mt, plt). When they are further subdivided by a transverse suture, Crampton, '09, refers to the subdivisions as the superior and inferior region of their respective medio- or pleurophragmite (medio- or pleurotergite). I shall refer to the subdivisions of the medio- and pleurotergite in the same manner (Fig. 1, spplt, iplt). In *Tipula* the pleurotergite is divided transversely into the superior pleurotergite and inferior pleurotergite (Fig. 1, spplt, iplt). In other Diptera such as *Leptis*, *Tabanus*, etc., the pleurotergite is subdivided by a longitudinal suture into the outer and inner pleurotergite (Figs. 2 and 11, oplt, inplt). Crampton, '09, previously used these adjectives to designate the outer and inner "pleurophragmite."

The scutellum projects laterally on both sides, until it meets the posterior margin of the wing. (Fig. 1, sl). The prescutum and postscutellum are often continued laterally on either side until they join the pleuron, although frequently these lateral prolongations become much reduced in size or split up into smaller pieces (Fig. 2, prsc, psl). Projecting internally, sometimes from the anterior margin of the tergum, sometimes from the posterior margin, or from both, is a process termed the phragma, which serves for the attachment of muscles. When the phragma is attached to the anterior margin of the tergum, it is termed the prephragma and when attached to the posterior margin, is termed the postphragma (Snodgrass, '10). The prescutum and postscutellum are frequently represented in the

tergum of insects simply by the inward projecting phragmas. In some insects the postscutellum is completely separated from the scutoscutellum by membrane. (Fig. 10, psl).

The old view that the tergum of adult insects consists of four consecutive transverse plates was proposed by Audouin, '24. He termed these plates the presecutum, scutum, scutellum and postscutellum, and this terminology has been retained though Audouin's general conception of the tergum, held until recently by most entomologists, is now obsolete. Other writers have given various names to the different tergal regions. Amans, '85, proposed the terms prodorsum, dorsum, postdorsum and subpostdorsum for the identical sclerites previously termed presecutum, scutum, scutellum and postscutellum by Audouin. Audouin's terminology has the right of priority, is widely accepted, has no undesirable features and should therefore stand.

WINGS. The wings of insects arise in two ways. In hemimetabolous insects they appear as outgrowths at the lateral margins of the meso- and metanotum. In holometabolous forms, they arise internally as the so-called wing-buds, appearing externally at or after pupation. At first the wings are filled with tracheæ, blood, tissue, etc. The tracheæ persist and are ultimately replaced by the veins or nervures of the adult insect wing, which serve as stiffening supports for the wing membrane. The blood and tissue gradually disappear and the two lateral surfaces of the sac-like outgrowth come together, forming the wing membrane.

The wings of adult insects are connected with the scuto-scutellum along its lateral margin, on the lateral margin of the tergum. They articulate with the pre- and post-alar processes, together with the small alar sclerites at the base of the wing (Fig. 10, pra, poa, sa, ba). Beneath they articulate with the pleural wing process (Fig. 10, plwp).

The wings are variously modified in different insects, forming the elytra of Coleoptera, the tegmina of Orthoptera, the halteres of Diptera, the hemielytra of Hemiptera and the hairy and scaly wings of Lepidoptera and Trichoptera. In such forms as Carabidæ, Ptinidæ, and weevils the hind wings are often lacking, owing to disuse, and the elytra in some forms fuse together thereby forming a solid covering for the hind wings (if present) and the abdomen. The general belief has always been that elytra are modified wings.

In homologizing the wings in the different orders of insects, by their venation, Comstock made use of the tracheæ, which occupy the position afterwards assumed by the principal veins in the wings of generalized insects. He termed the veins costa, subcosta, radius, media, cubitus, and anals. This terminology is quite widely accepted and generally used, especially for Lepidoptera.

Several theories have been proposed to account for the origin of the wings. Gegenbauer, '70, claimed that the wings developed from tracheal gills. Palmen, '77, discredited this theory by demonstrating that tracheal gills occur on the sternum, abdomen, tergum, pleuron and in the anal region; that tracheal gills and the closed tracheal system is a secondary adaptation to the aquatic life of the larva and that aerial respiration was probably the primitive condition.

Plateau, '71, thought that the wings developed from hypertrophied spiracles. Müller, '75, from a study of the development of the wings of *Calotermes*, concluded that they arose as lateral outgrowths of the dorsum. To this theory Pancritius, '84, adds the idea, that the primitive outgrowth of the body wall may have developed into a protective body covering like an elytron, which became modified to form the wings. Packard, '98, accepted and developed Müller's theory. He apparently thought that primitive winged insects had lateral extensions of the thoracic segments, which acted as a sort of parachute and which later gave rise to true wings. Palaeontological records show that some insects had lateral extensions of the pronotum which may have served as a parachute and that many of the earliest of the Pterygota have well developed wings, which seem to have articulated with the thorax. Packard's theory is plausible.

PLEURON. The pleuron in a restricted sense consists of the sclerites lying between the dorsum and sternum and forming the lateral wall of any thoracic segment. In nearly all insects it is composed of two sclerites, the episternum or anterior sclerite and the epimeron or posterior sclerite (Fig. 8, *es*₁, *em*₁). In the higher forms, the pleuron is usually connected with the tergum by prolongations of the prescutum and postscutellum, the latter often extending downward for some distance and fusing with the pleuron, in which case it is frequently mistaken

for a part of the pleuron (Figs. 2 and 11, psl, prsc). These prolongations of the tergum are usually lacking in the lower forms. In other insects they may be much reduced in size or split up into smaller pieces.

The episternum and epimeron are separated externally by a suture, termed the pleural suture, which extends from the pleural wing process or fulcrum to the pleural coxal process (Fig. 1, pls₂). Internally these two sclerites may be readily distinguished from each other by a strongly chitinized ridge variously termed the pleural ridge, entopleuron or apodeme, which likewise extends from the pleural wing process to the pleural coxal process.

The pleuron bears three processes which usually have an inward projection for the attachment of muscles. Above is the pleural wing process which serves for the articulation of the wing (Fig. 2, plwp). It consists of a dorsal prolongation of the pleuron, of variable length, through which runs the pleural suture externally and the entopleuron internally. On the lower margin of the pleuron is the pleural coxal process, with which the coxa articulates (Fig. 4, exp). It is similar to the pleural wing process and has the pleural suture and pleural ridge extending through it. The pleural process or pleural arm (Snodgrass, '10) is situated a short distance above the coxal process. It projects inward and downward from the entopleuron. Usually it rests against the furca (an inward projecting process of the sternum, termed the apophysis) and frequently fuses with it (Fig. 12, f).

Along the dorsal edge of the pleuron are generally found three or four small sclerites. Two of these, the basalar plates (Crampton, '14) are generally found in front of the pleural wing process, and are termed by Crampton, '14, the anterior and posterior basalar sclerites, terms which will be used in this paper (Fig. 2, pba, aba). Behind the wing fulcrum there is usually one, sometimes two of these sclerites, which are termed subalar plates (Crampton, '14, Fig. 2, sa). Lowne, '90, in his book on the Blow-Fly, terms the subalar plate, the "costa." Snodgrass, '08, terms it the "postepimeron" and Crampton, '09, the posterior "costal sclerite." Verhoeff termed the anterior basalar plate, the "alarpleura." Snodgrass, '10, termed all these plates the "paraptera." Those situated in front of the wing process, he called the preparaterum or episternal paraptera

and those behind the postparapterum or epimeral paraptera. Snodgrass claims in his "Anatomy of the Honey Bee," pp. 20, footnote (a), that Audouin, '24, termed these plates the paraptera and hence Snodgrass would retain this term. This, however, is not the case. Audouin, '24, termed the small sclerite which sometimes extends along the anterior edge of the episternum the "paraptere" and confuses it with the tegulae and other sclerites at the base of the wing. Later Audouin, '32, clearly defined the "paraptere" as the tegulae (1832 Audouin, Exposition de L'anatomie du Thorax. par W. S. MacLeay, Accompagnee de notes par M. Audouin. Ann. Sci. Nat. XXV, Ser. 1, pp. 41, footnote.) He says: "In fact I consider as the paraptere the small piece so visible in the Hymenoptera and in the Lepidoptera, which covers the base of the fore wings and which has been designated by the name ecaille, epaulette or squamala." Jordan, '02, terms the subalar plate the "parasternum" and also applies this term to the anepisternum (upper portion of the episternum) in his figures. His homologies of the sclerites are evidently incorrect. Berlese, '06, termed the basalar sclerites the "acrosterno o prefulcro (anteriore e posteriore)." The subalar sclerite he terms the "paraptero," (Gli Insetti, pp. 244). "Prefulcro" is a good term for the basalar sclerites, as it designates their position in front of the wing fulcrum, but the term "paraptero" does not seem desirable. Crampton's, '14, term, subalar sclerites, is far more suitable since it exactly describes the position of these sclerites.

The pleuron may be more or less modified in different insects. In the mesothorax of some Diptera, the parts have shifted forward, thereby causing the pleural suture to become twisted and curved (Fig. 11, pls₂). In Odonata the pleuron assumes an oblique position and as a result, the episternum becomes dorsal and the epimeron ventral. In other insects the pleural sclerites are variously modified in shape and size.

Crampton, '08, was the first to suggest that the pleuron probably consisted originally of but one plate and that the episternum and epimeron may have been formed by the infolding of the integument, due to muscle stress. This view was later developed by Snodgrass, '09. In such insects as *Eosentomon*, *Leuctra* (prothorax), acridid nymphs and *Anisolabis*, the pleuron is apparently represented by a single plate, in which the pleural suture is present. If the pleuron was originally a single plate,

which seems very probable, then the pleural suture probably arose by an infolding of the integument of this plate. In the pleuron of *Periplaneta* for example, the line which represents the pleural suture is clearly formed by the two external lips of the infolded integument coming together and resting against each other, but the edges or lips do not fuse. On pressing the edges or lips of the fold apart, a large hollow pocket will be seen, at the bottom of which is the apodeme and the pleural arm. The pleural arm is sometimes hollow and usually chitinized. These conditions would be produced by the infolding of the integument of the pleuron, possibly due to muscular stress, possibly from other causes. This is the simplest and most probable explanation.

Some investigators regard the pleuron as being formed by two sclerites coming together, fusing and the edges rolling inward to form the pleural suture and apodeme. This view seems very improbable. It is complicated and does not account for the single plate representing the pleuron in *Eosentomon*, *Leuctra*, etc. Furthermore, two sclerites whose edges meet and fuse are not apt to be plastic enough to permit their being drawn out into a prolongation forming the pleural arm and pocket, but would more probably be firm and resistant.

Audouin, '24, considered the pleuron as composed of three sclerites, the anterior or episternum, the posterior or epimeron and the peritreme or spiracle bearing sclerite. This terminology is widely accepted (with the exception of peritreme) in general use and there is no valid reason for changing it as some writers have done, since this only leads to confusion. Kirby refers to the epimeron as the pleura. Burmeister thought the pleuron was part of the sternum and others regard it as the basal sclerites of the leg.

Heymons, '99, in his "Beitrage zur Morphologie und Entwicklungsgeschichte der Rhynchoten," pp. 443, in discussing the sclerites of *Nepa*, was the first to use the term subcoxa and applied it to what he thought was the mesothoracic pleuron, consisting of episternum and epimeron. A study of *Nepa* shows that Heymons' subcoxa actually consists of the mesothoracic episternum, the precoxal bridge or precoxale (Crampton, '14), and possibly the trochantin. The sclerite in *Nepa* which Heymons thinks is the metathoracic pleuron, he terms the "pleurite," pp. 376. This sclerite is not the metathoracic

pleuron, but is the epimeron of the mesothorax. It extends posteriorly as a sort of flap covering the metathoracic epimeron, which would easily escape notice unless closely observed. Heymons was confused in the use of his own term subcoxa, which has led to its misinterpretation by other workers. Enderlein and also Berlese thought the "subcoxa" corresponded to the trochantin. Börner considered it equivalent to his "merosternum" or pleuron. Verhoeff regarded it as representing the coxopleure (episternum) and trochantin.

EPIMERON. The epimeron varies greatly in size and shape in different insects. Most writers consider it as a single sclerite, which is usually the case (Fig. 8, em_1).

In the prothorax of *Periplaneta* there is a small sclerite, which has become split off from the posterior edge of the epimeron, and may be termed the postepimeron (Fig. 3, pem_1). Snodgrass, '08, applied this term to the subalar plate. It has since been discarded and so far as I know, has never been applied to any other sclerite. Therefore, as it describes the exact position of the sclerite, which has become detached from the posterior edge of the epimeron, I have adopted it to designate the sclerite in question. In the prothorax of *Capnia* (Fig. 4, pem_1), there is a large sclerite comparable to the postepimeron, which is likewise split off from the posterior edge of the epimeron and extends behind the coxa until it meets the furcasternite, thereby forming the postcoxal bridge or postcoxale (Crampton, '14). In the mesothorax of *Corydalis* (Fig. 10, pem_2) the epimeron is a single sclerite, a projection of which extends behind the coxa. In many Coleoptera and Tenthredinidæ (prothorax of *Dolerus* (Fig. 12, em_1) the epimeron is greatly reduced in size.

The epimeron is often divided into two sclerites by a transverse suture. This condition can be seen in the mesothorax of such insects as *Mantispa*, *Chrysopa*, *Leptis*, and in some Tipulidæ and Tabanidæ (Figs. 1 and 2, em_2). In Diptera the lower portion of the epimeron of the mesothorax is usually fused with the meron, being separated by a suture, although the suture is often wanting (Figs. 1 and 11, mp). Packard, '80, seems to have been the first to apply terms to the subdivisions of the epimeron. In describing the thorax of *Mantispa*, he termed the upper region, the sur-epimeron and the lower the

infra-epimeron. Crampton, '08, used the terms hyper- and hypo-epimeron for these regions, but on account of the similarity of the terms he later (Crampton, '09), discarded them, substituting in their place anepimeron and katepimeron.

Osten-Sacken's terminology has been widely used for the Dipteron thorax and is very good. Crampton, '14, retains it in a slightly modified form, viz.: changing the ending from pleura to pleurite. Thus in the Diptera, Crampton, '14, terms the upper region of the epimeron the pteropleurite (situated beneath the wing base (Fig. 1, ptp) and the lower region meropleurite (usually fused with the meron, especially in Diptera (Figs. 1 and 11, mp). These terms will be adopted in this paper.

Some Diptera such as *Tipula*, *Chrysopa*, etc., have the lower portion of the epimeron separated from the meron by a suture. In such cases the term katepimeron (Crampton, '09) will be applied to the lower portion of the epimeron (Figs. 1, 2 and 13, kem). The term meropleurite will be applied to the katepimeron plus the meron whether these sclerites are completely fused into one as in the mesothorax of *Tabanus* (Fig. 11, mp), or separated by a suture as in *Tipula* and *Chrysopa* (Figs. 1 and 13, mp). In either case the meropleurite represents identical regions (Figs. 11 and 13, mp).

The subalar plate or its representative is always present behind the pleural wing process (Figs. 1, 2 and 11, sa). It may be partly fused with the epimeron or entirely separated from it by membrane. Both of these conditions can be found in the Diptera (*Leptis*, *Tabanus*, etc., Figs. 1 and 2, sa). Sometimes the subalar plate is divided into two sclerites as in some of the Plecoptera, and in that case will be termed anterior and posterior subalar sclerites (Crampton, '14). In some Leptidæ and Tabanidæ, there is a cleft immediately below the subalar plate (Figs. 2 and 11, sa), which is prolonged downward into the epimeron (pteropleurite, ptp) for a short distance in the form of a suture, but the internal ridge of this suture is not continuous with the pleural suture. Snodgrass, '10, mistook this suture for the pleural suture, which it closely resembles when viewed externally. By carefully examining a specimen which has been boiled in caustic potash, the mistake will be readily discovered and the real pleural suture can be easily traced by means of the apodeme, from the coxal process into the pleural wing process (Figs. 2 and 11, pls₂).

In studying the thorax in a series of insects such as *Mantispa*, *Chrysopa*, *Tipula*, *Leptis* and *Tabanus*, it will be observed that there is a gradual shifting forward of the sclerites, being most pronounced in the mesothorax (Figs. 13, 1, 2 and 11). This causes the pleural suture of the mesothorax to become more or less crooked as shown in Figs. 1, 2 and 11, pls₂.

Starting at the upper end of the mesothoracic wing fulcrum of *Tabanus* (Fig. 11, plwp) the pleural suture (pls₂) runs downward and slightly forward in a more or less curved line until it meets the sternopleurite (lower region of the episternum). (Fig. 11, stp). Here it turns almost at right angles and runs posteriorly to the meropleurite (lower portion of epimeron), (Fig. 11, mp) and thence downward and slightly backward to the coxa. This condition is very confusing and hard to see, unless the specimen is first boiled in caustic potash, in which case the pleural suture is readily observable.

In Diptera the meron is often fused with the lower region of the epimeron, forming the meropleurite (Fig. 11, mp), but as the former sclerite is usually closely connected with the coxa it will be treated under the heading Coxa.

Audouin, '24, applied the term epimeron to the sclerite immediately posterior to the episternum. This term has been generally accepted and used by nearly all subsequent entomologists. The epimeron was termed by Burmeister, '32, the "pleura;" by Verhoeff, '03, the "anopleure;" by Amans, '85, the "postpleuron," and by Heymons, '99, the "pleurite." Hammond, Brauer and Lowne who have worked on the Dipteron thorax, where the epimeron is often subdivided into two sclerites, have applied the term epimeron to various thoracic sclerites and the terminology has been greatly confused. Osten-Sacken's terminology for the thorax of Diptera is very good and should be retained. Crampton, '14, in a review of the Dipteron thorax has retained this terminology slightly modified as previously stated. This terminology should also be applied to all insects in which the epimeron and episternum are subdivided as in *Mantispa*, *Chrysopa*, etc., since it has been established by wide-spread acceptance among those working on Diptera and should be made a uniform terminology for all insects with a thorax of this nature, as far as possible.

The term parapleuron has given rise to much confusion among morphologists. It was first applied to the entire pleural

region by Knoch. Kirby termed the epimeron and episternum, the parapleuron, an interpretation accepted by Smith, '06. Burmeister and also Voss applied the term parapleuron to the episternum. Kolbe used it for a sclerite occurring in beetles, situated behind the wing and between the tergum and pleuron. Ritter's parapleuron is equivalent to the anepisternum or upper region of the episternum. Others have used the term parapleuron to designate various sclerites of the thorax. At present there is no uniformity of opinion concerning the application of the term even among Coleopterologists, by whom it is chiefly used.

EPISTERNUM. The episternum is also subject to great variation in insects. It may consist of a single sclerite as in the earwig (Fig. 8, es_1), or it may be subdivided into an upper and lower region as in *Mantispa*, *Chrysopa*, *Corydalis*, *Tipula*, etc. (Fig. 2, es_2). The suture which divides the episternum into two regions may extend clear across, making a complete division, as in the mesothorax of *Tabanus* (Fig. 11, g) or only part way, as in the mesothorax of *Tipula* (Fig. 1, g). In *Chrysopa* and *Mantispa* (Fig. 13), the division is represented by a narrow strip of chitin of varying width, extending inward midway between the two subdivisions. This strip is probably a part of the episternum which has become fused with the precoxal bridge (Crampton, '14). It may, however, belong entirely to the precoxal bridge, a projection of which extends between the two subregions, but this latter alternative is very improbable. The formation of this region in other insects seems to indicate that it is a part of the episternum. Crampton, '09, applied the term "median region," to this narrow strip of chitin. This seems to be the only term which has been applied to it. It hardly seems necessary to give this region a name and consequently none will be used in this paper.

When the episternum is subdivided, a condition found in a great many insects, the lower division may be fused with the sternum (Figs. 1, 2 and 11, stp). The episternum is separated from the epimeron by the pleural suture. In all insects, both the episternum and epimeron extend from the coxal process to the pleural wing process. This condition can be plainly seen in most insects, but in some such as *Tabanus*, etc. (Fig. 11, stp), the lower portion of the episternum of the mesothorax has

become fused with the sternum. Many workers have considered this fusion product of sternum and lower portion of the episternum as the entire sternum and accordingly termed it the sternum. This misinterpretation has led to great confusion in the terminology. In the mesothorax, Lowne termed this composite region the "mesoplastron." He also applied the term, "metaplastron" to the meropleurite (lower portion of epimeron fused with the meron) of the mesothorax (Fig. 11, mp). Chabrier had originally used the term "plastron" to designate the pleuron of the prothorax, so that Lowne is incorrect in stating that the "mesoplastron" is the "plastron" of Chabrier. Packard, '80, used the terms sub- and infra-episternum to designate the fusion product of the sternum and lower region of the episternum. Snodgrass, '10, and several other workers termed it the "sternum." Osten-Sacken, '89, used the term "sternopleura." Crampton, '09, designated it by the component parts entering into its composition, but later Crampton, '14, adopted Osten-Sacken's terminology, slightly modified, calling it the sternopleurite. The latter term will be used in this paper.

The lower portion of the episternum in *Chrysopa* and like insects has a new region marked off, which is composed of a different combination of sclerites than the region representing the sternopleurite in *Tabanus*, and hence has been termed pleurotrochantin, (Crampton, '14) (Fig. 13, pltn). This term will be retained in this paper. The pleurotrochantin is composed of the lower part of the episternum, most of the trochantin and the antecoxale. The term sternopleurite, however, will still be applied in *Chrysopa* and like insects, to the pleurotrochantin plus the precoxale and sternum (Fig. 13, stp), since this region would then be identical with the sternopleurite of Diptera (Fig. 11, stp). In this way a uniformity of terminology is retained.

The upper region of the episternum is a more or less square sclerite, which has become pushed forward in the mesothorax of such insects as *Tabanus* (Fig. 11, esp), due to the shifting forward of the parts as previously mentioned. The upper margin of this sclerite and also the pteropleurite (upper portion of the epimeron) often contain clefts of varying depth and width (Figs. 2 and 11). The shifting forward of sclerites naturally led to their misinterpretation by different workers and finally

resulted in a confused terminology. Packard, '80, termed the upper region of the episternum, the "sur- and supra-episternum." Hammond, '81, called it the "parapteron." Brauer, '82, and several other workers called it the episternum, while Snodgrass, '09, included a portion of the pteropleurite (upper region of the epimeron) and the upper region of the episternum together, as the episternum. Lowne, '90, termed it the lateral plate of the "mesosternum," Petri, '99, the "antepleura," borrowing Amans '85, term for the entire episternum, (antepleuron). Osten-Sacken, '84, termed it the "mesopleura," which is inappropriate, because it is not the entire mesopleuron. Crampton, '08, called it the "hyper-episternum" and later, Crampton, '09, the "anepisternum." I shall adopt for it the term anepisternum. In *Chrysopa*, *Mantispa*, etc., (Fig. 13, esp, ptp) the terms anepisternum and also pteropleurite have been used for the upper portions of the episternum and epimeron, since these regions are homologous with those found in Diptera (Fig. 11, esp, ptp).

In the meso- and metathorax of *Periplaneta* the episternum consists of one sclerite, which is fused with the precoxal bridge or precoxale (Crampton, '14) (Fig. 3, es, es₃). The trochantin is partially attached to the episternum in the prothorax (Fig. 3, tn₁). The episternum, together with the epimeron form a deep hollow pocket by the infolding of the integument, which bears internally the pleural process. The episternum in the earwig consists of a single sclerite (Fig. 8, es₁).

In *Capnia* the prothoracic episternum consists of one piece (Fig. 4, es₁). The meso- and metathoracic episternum is divided by a suture into an upper and lower portion (Fig. 4, esp, pltn) giving a condition comparable to that found in *Chrysopa* (Fig. 13, esp, pltn). Here also we have the beginning of a condition similar to that found in *Tabanus* (Fig. 11, esp, stp). The fusion of the sternum with the lower portion of the episternum, precoxale, etc., suggests the probable formation of the sternopleurite (Figs. 1, 2 and 11, stp).

In *Corydalid* the condition of the episternum in the mesothorax is similar to that found in *Capnia* and *Tabanus*. (Fig. 10, esp, stp). The suture dividing the episternum becomes more pronounced and takes the form of a deep cleft. The precoxale, sternum and episternum become more closely fused.

Packard, '80, in his figures of *Corydalis* shows the episternum extending from the coxa to the wing process. He also includes the trochantin and precoxal bridge as part of the episternum. Crampton, '09, considered the episternum as extending from the coxal process to the pleural wing process. Snodgrass, '09, regarded the anepisternum (upper portion of episternum) in *Corydalis*, as the entire episternum (Fig. 10, esp). The episternum, however, extends from the coxal process to the pleural wing process, as is very clearly illustrated in *Periplaneta*. Most writers fail to take this fact into consideration and consequently the resulting misinterpretation and confusion.

In *Dictyophora* and *Dissosteira* the sternum, episternum and precoxale are closely united. This condition is more or less pronounced in the various insect orders. In the pro-, meso- and metathorax of *Forficula* (Fig. 8, pc₁, pc₂, pc₃) and in the mesothorax of *Gryllus*, (Fig. 7, pc₂) the precoxale becomes split up and is not fused with the sternum. In the prothorax of *Gryllus*, however, the episternum, precoxale and sternum are closely united (Fig. 7, pc₁, es₁, vs₁).

Audouin, '24, termed the anterior plate of the pleuron the episternum. This term is still in use and accepted by everyone. When the episternum is subdivided it is necessary to use other terms to designate the subdivisions, as previously discussed in the case of *Tabanus*, *Mantispa*, *Chrysopa*, etc. Burmeister, '32, termed the episternum the "parapleura." Packard, '80, called the upper portion the sur- and supra-episternum and the lower portion the sub- and infra-episternum, using the former and also the latter terms interchangeably. Packard studied a large number of insects and used the terms, "pleurites" and "sternites," in his terminology. Although his homologies of the sclerites are incorrect in many cases, his terminology has many good points. His work on the whole is very good and has not been accorded sufficient attention. Amans, '85, termed the episternum the "antepleuron." Jordan, '02, applied the terms "para-sternum" and "episternum" to the anepisternum (upper portion of episternum). The term "parasternum" he also applies to the basalar plate. The sternopleurite (lower portion of episternum fused with a part of the sternum), he terms "hyposternum." He confuses his own terms by misinterpreting the sclerites in different papilionids. In *Forficula*,

Verhoeff, '03, termed the episternum the "coxopleure," while in the roach his "coxopleure" consists of the precoxale together with the episternum.

Audouin's, '24, term episternum is satisfactory and generally accepted, while the other terms applied to the episternum are useless synonyms. This confusion was brought about by the misinterpretation of sclerites and by the tendency of writers to set forth their own ideas of the terminology. In doing this, they have invented new terms to suit their respective views and have not given sufficient attention to the work and terminology of previous investigators.

PRECOXALE. The precoxale is situated in front of the coxa and is either united or completely fused with the episternum. The end of this sclerite nearest the sternum may be free as in *Periplaneta* (Fig. 3, pc₁), or it may be united or fused with the sternum as in the mesothorax of *Capnia* (Fig. 4, pc₂), thereby forming a bridge connecting the episternum with the sternum. Hence the term precoxal bridge or precoxale of Crampton, '14. The portion nearest the sternum is sometimes split transversely into one or two small sclerites, as in the mesothorax of *Forficula* (Fig. 8, pc₂). In other cases the precoxale is entirely fused with the episternum and sternum as in the Coleoptera, Formicina, Diptera, etc. (Fig. 10, pc). A portion of it may fuse with the episternum and a portion with the sternum as illustrated in the metathorax of *Forficula* (Fig. 8, pc₃), or it may disappear as in the prothorax of *Macroxyla* (Fig. 14). The division between sternum and episternum in the metathorax of *Forficula* (Fig. 8, es₃, vs₃) is probably secondary, although this condition is open to other interpretations.

The precoxale, while constant in position is extremely variable in size and form. In *Periplaneta*, which is admittedly a very primitive insect, the precoxale is similar in all three thoracic segments, its dorsal portion being always fused with the episternum, except in the prothorax, while the ventral portion borders on the sternum, but is not strongly connected with it (Fig. 3, pc₁, pc₂, pc₃). In the meso and metathorax, there is a deep cleft in front of the pleural wing process, at the mouth of which is a small sclerite, comparable to one of the basalar sclerites, previously discussed (Fig. 3, pba₂, pba₃).

The other basalar plate is probably represented by a small sclerite, which is marked off on the upper corner of the precoxale by a heavy suture (Fig. 3, aba₂, aba₃).

In *Periplaneta* there is a suture which divides the meso- and metathoracic episternum and precoxale (Fig. 3, 0). Part of it can be plainly seen and the other part (represented by the dotted line) is rather faint and hard to see. If the specimen is first boiled in caustic potash, the suture can be more easily distinguished. This suture suggests very strongly the beginning of the formation of a sclerite, comparable to the anepisternum (upper portion of the episternum) of the Diptera. In some roaches it is represented by one heavy suture, plainly seen throughout its entire length.

Along the anterior margin of the metathoracic precoxale there is marked off a small sclerite, which I shall term the pre-episternum (Fig. 3, pes₃). It seems to be homologous with Audouin's '24, "hypoteron." Hopkins first used the term pre-episternum to designate the sclerite which Audouin termed the "hypoteron," in *Dytiscus* and it should be applied to that sclerite only. Jordan, '02, terms the pre-episternum the "peristernum." Snodgrass, '09, has used the term pre-episternum, but is so inconsistent in its application that it is hard to tell what his pre-episterum represents. In his various figures, he has designated the episternum, precoxale, one of the basalar sclerites and the pre-episternum proper, by the term pre-episternum. In his "Thorax of the Hymenoptera," he calls the pre-episternum the "prepectus."

Immediately posterior to the precoxale in *Periplaneta*, a narrow sclerite is marked off, the antecoxale of Crampton, '14, whose term I shall adopt for this sclerite. This sclerite is folded under the precoxale in the prothorax (Fig. 3, ac₁) and is homologous with the lateral portion of the antecoxal piece of Coleoptera. It is connected with the precoxale in *Periplaneta* by very thin or non-pigmented chitin, not by membrane. This suggests that it is probably derived from the precoxale by a secondary longitudinal marking off. In other insects it has either disappeared or become fused with other sclerites which surround it, such as the trochantin, precoxale, etc. The antecoxale was termed by Walton, '00, the "antecoxale piece;" by Comstock, '02, the "second antecoxale piece," and by Crampton, '09, the "antecoxale laterale." Verhoeff, '03,

terms it the "katopleura" in the roach, but in the Forficulidae he applies the term "katopleura" to an entirely different sclerite.

In *Forficula* the condition is quite different from that found in *Periplaneta*. In the prothorax the precoxale may have fused with the trochantin and episternum following which there was a secondary marking off, of a triangular sclerite, consisting partly of trochantin and precoxale (Fig. 8, tn_1), and of two narrow sclerites extending along the anterior margin of the episternum (Fig. 8, pc_1), which represent a part of the precoxale, the rest of it having fused with the episternum. Another view is that the triangular sclerite (Fig. 8, tn_1) represents the entire trochantin and that the two narrow sclerites along the anterior edge of the episternum represent the entire precoxale (Fig. 8, pc_1), which has become reduced in size. The precoxale in *Diapheromera* is very narrow and reduced in size, thus showing that such a condition is not at all abnormal or improbable.

In the mesothorax the precoxale has become split transversely into two sclerites (Fig. 8, pc_2). For the sclerite nearest the sternum, I suggest the term sternocoxale (Fig. 8, stc) and for the sclerite nearest the pleuron, the term pleurocoxale (Fig. 8, plc). In the metathorax a portion of the precoxale may have fused with the episternum, sternum and trochantin (Fig. 8, pc_3). How much has fused with each, it is impossible to say. Another view is that the pleurocoxale has fused with the episternum; the sternocoxale with the sternum and the triangular sclerite (Fig. 8, tn_3) represents the entire trochantin. In the thorax of *Forficula* there is no complete connection between the episternum and sternum.

There is a small sclerite between the pleural region and sternum in the mesothorax of *Gryllus*, which is homologous with the sternocoxale (Fig. 7, stc). Voss termed it the "coxosternite."

In *Locusta*, *Capnia*, *Corydalis*, and many Lepidoptera, Diptera, Coleoptera, etc., the precoxale is usually fused with the episternum and sternum, forming a continuous bridge between them (Fig. 4, pc_2). Secondarily formed sutures often appear in this bridge or precoxale, as in *Capnia*, *Corydalis*, etc.

The precoxale shows an interesting transition in the prothorax of sawflies. In *Abia* and also *Cimbex*, the episternum and sternum are connected by the precoxale (Fig. 15, pc). The

latter is in the process of disappearing in *Dolerus* and is represented by a small sclerite on either side of the sternum (Fig. 12, pc). These small sclerites are not connected with either the sternum or episternum, but lie half way between them. In *Macroxyla* all trace of the precoxale is lost (Fig. 14). There is no indication of the connecting bridge between episternum and sternum, but the sternum is larger than in *Dolerus* or *Abia* and probably represents the fusion product of a part of the precoxale and sternum (Fig. 14, vs).

The terminology of the above discussed sclerites is somewhat confused. The precoxale was termed "laterale" by Crampton, '09 and "precoxal bridge" or "precoxale" by Crampton, '14. The pleurocoxale was termed "katopleura" by Verhoeff, '03, in the Forficulidæ, and in the Blattidæ he applies the same term to an entirely different sclerite, showing that his homologies of the thoracic sclerites are evidently incorrect. It was termed "episternal laterale" by Crampton, '09, and "lateropleurite" by Crampton, '14. The sternocoxale was termed "vorplatte," by Verhoeff, '03, "sternal laterale" by Crampton, '09, and "laterosternite" by Crampton, '14.

In introducing the terms pleurocoxale and sternocoxale, an effort has been made to improve the terminology of these sclerites. They are more or less closely associated with the precoxale and antecoxale of Crampton, '14, and all are situated near the base of the coxa. Hence the sclerites composing this region have been given a uniform ending, which with the prefix, denotes quite accurately the respective positions of these sclerites. The term trochantin is so widely known, accepted and used that it would not be advisable to change it. This, however, does not apply to the other sclerites mentioned above.

TROCHANTIN. The trochantin is a more or less triangular shaped sclerite situated at the base of the coxa (Fig. 3, tn₁). It varies in size being quite large in some insects (*Periplaneta*, Fig. 3, tn₂) and small in other forms. (*Tipula*, *Capnia*, etc., Fig. 4, tn₁). In some forms, such as in the prothorax of *Periplaneta*, *Capnia*, etc., the basal portion of the trochantin is fused for a short distance with the episternum (Fig. 3, tn₁). In other insects it is partially or completely fused with the episternum and precoxale or else has disappeared. These various

conditions of the trochantin are illustrated in such insects as *Corydalis*, *Capnia*, some Orthoptera, Trichoptera, Diptera, Coleoptera, etc. When the trochantin is present and not completely fused with other sclerites, it always articulates with the coxa.

In the prothorax of *Periplaneta* the trochantin has become transversely split into two sclerites, the upper and larger of which has been termed trochantinus major (Crampton, '09) (Fig. 3, tnm), and the lower and smaller the trochantinelle (Crampton, '14) (Fig. 3, tnl). Other writers consider the trochantinelle as the entire trochantin, but this is a mistake as one can readily see by comparing the trochantin of the prothorax with that of the meso- and metathorax, in which it is not divided transversely into two sclerites. The end of the trochantin which articulates with the coxa is constant in position in all three thoracic segments and bears at its extremity a small inward projecting process (Fig. 3, atn). In the prothoracic segment the trochantin is fused with the episternum for a short distance and is separated from the rest of the episternum and antecoxale, partly by suture and partly by membrane (Fig. 3, tn₁). In the meso- and metathorax, the trochantin is entirely marked off from the episternum and antecoxale by membrane (Fig. 3, tn₂).

In *Periplaneta*, the trochantin also has a distinct, heavy, longitudinal suture, dividing it into an anterior and posterior region, termed ante-trochantin and post-trochantin (Crampton, '14) respectively (Fig. 3, atn, ptn). This suture occurs in the trochantin of the pro-, meso-, and metathorax of the roach and can be plainly seen. In the prothorax (Fig. 3, tn₁) where the trochantin is divided into two sclerites, this longitudinal suture extends through both, thus showing that these two sclerites are equivalent to the sclerites in the meso- and metathorax which everyone admits is the entire trochantin.

In the mesothorax of *Corydalis* the trochantin is partly fused with the episternum and antecoxale. A part of it which corresponds to at least a portion of the trochantinelle, projects free and is partly constricted off from the rest of the trochantin (Fig. 10, tnl). This would indicate that the trochantinelle in the prothorax of *Periplaneta* is a detached portion of the trochantin. In *Corydalis* the portion of the trochantin which

projects free is also divided longitudinally by a suture into an anterior and posterior region (Fig. 10, *tnl*). It articulates with the coxa and has an inward projecting process at its extremity. These features are also present in the trochantin of *Periplaneta*.

The trochantin of the pro- and metathorax in *Forficula*, assumes the shape of a triangle (Fig. 8, *tn*₁, *tn*₃). This sclerite may be the entire trochantin or it may be the fusion product of the trochantin and part of some other sclerite such as the precoxale or antecoxale. In the mesothorax there are three small sclerites between the trochantin and the coxa, one of which is probably a detached portion of the coxa and the others of the trochantin (Fig. 8, *tn*₂).

Sharp, '95, in discussing the thorax of insects (Camb. Nat. Hist. vol. V, pp. 222) figures the base of the front leg and part of the prothorax of *Blabera gigantea*. He finds the homologies of the thoracic sclerites difficult to determine and his figure is wrongly labeled. The region marked "epimeron" is a part of the trochantin; the "fold of the pronotum" is the epimeron and the sclerite he has termed the trochantin is only a part of the trochantin, viz., the trochantinelle.

Packard, '98, terms the meron the "trochantin." Jordan, '02, terms a small sclerite lying along the anterior margin of the coxa, the "trochantin." Comstock, '02, termed the post-trochantin the "trochantin;" the ante-trochantin, the "first antecoxal piece," and the antecoxale, the "second antecoxal piece." Berlese, '06, terms the trochantin the "subcoxa." Snodgrass, '09, Verhoeff, '02-'04, and others have termed the trochantinelle, the entire trochantin. Crampton, '09, used the term, "trochantinus minor," to designate the trochantinelle and the terms "coxal trochantin" and "antecoxal trochantin" to designate the post- and ante-trochantin.

COXA. The coxa is the basal segment of the leg and the only one, which it will be necessary to consider in this paper. It varies greatly in size and shape in different insects, but is always constant in position and serves as a landmark in homologizing the thoracic sclerites. In some forms it is undivided and in others it is composed of two or more pieces (Fig. 8, *cx*₃). It articulates with the coxal process and with the trochantin when the latter is present.

In *Periplaneta*, *Corydalid*, *Dictyophora*, etc., a narrow, heavily chitinized area is marked off by a suture along the anterior margin of the coxa (Fig. 10, cm). Crampton, '09, termed this region the "Coximarginal sclerite." There is also found in some insects a small sclerite with an inward projecting process, which is free, absent or attached to the anterior margin of the coxa, and is comparatively unimportant.

A glance at the coxa of the meso- and metathorax of *Periplaneta* will show that it is partly divided into an anterior and posterior region (Fig. 3, m. vcx). The posterior region will be termed the meron (Walton, '00) and the anterior, the veracoxa (Crampton '14). The suture which marks the divisions of the coxa, is apparently a continuation of the pleural suture. In *Periplaneta* the meron is partly fused with the coxa and partly divided from it by a suture (Fig. 3, m). The meron when present appears to be developed in the meso- and sometimes in the metathorax. I have never observed its presence in the prothorax and in some Diptera it is absent in the pro- and metathorax. Hence the development of the meron may possibly have some connection with the development of the wings. The coxa was probably originally one undivided sclerite and the meron has been derived from it secondarily. Where the meron does not occur, the coxa probably represents a persistent primitive condition, such as frequently occurs in insects.

In some insects the meron is completely marked off from the coxa by a suture (Fig. 4, m) and in many forms such as Diptera, it has become drawn upward or enlarged, so that it extends into the epimeral region and is often fused with the epimeron (Figs. 1, and 2, m). This has led to its misinterpretation in the Diptera by Snodgrass, '09, and others, who have considered it to be part of the sternum. The meron is separated from the sternum by membrane in such insects as *Tabanus*, *Tipula*, etc., and the sternum can be plainly seen to extend behind the meron (Fig. 11, msst).

Snodgrass, '09, considered the meron as derived from the epimeron. In the larva of *Corydalid*, he finds the epimeron marked off into an upper and lower region. In the pupal stage he finds that the lower portion of the epimeron has extended behind the coxa and partly fused with it. In the adult, he

finds this region has fused entirely with the coxa and is separated from the epimeron by membrane. He also finds similar conditions in the larval, pupal and adult stages of Trichoptera. It seems more probable however, that the meron is part of the coxa and derived from it, as the condition found in the roach plainly indicates. The roach is also a more primitive insect than the Trichoptera, etc. In some insects (*Tipula*, *Mantispa*, etc.) the epimeron is divided into an upper and lower region and the meron is also present. This would probably not be the case if the meron were equivalent to the lower portion of the epimeron (Figs. 1 and 13, m).

The position of the coxa in its various relations to the other parts of the thorax in different insects, has led to the formulation of various theories from time to time.

Thus Miall and Denny, '86, from a study of the roach, concluded that the sclerites at the base of the leg, represent two basal leg joints, which became attached to the thorax.

Heymons, '99, in his studies on *Nepa* designated the sclerites at the base of the leg (episternum, precoxale, etc.) as the "sub-coxa," and adopted Miall and Denny's view, that this region represents the basal portion of the leg.

Several writers including Hansen, Jourdain, Börner and Henneguy, have compared the styli found on the meso- and metathoracic coxæ in certain insects, to parts (exopodite, epipodite, etc.) of the crustacean leg. Banks, '93, considered the styli as vestigial legs and Verhoeff, '02-'04, regarded them as homologous with the coxal organs of Myriopoda.

Walton, '00, considered the meron as a vestigial leg, but has since retracted this statement.

Most of the above mentioned theories have already been discussed under the heading, Historical Review, and it will not be necessary to consider them further here.

STERNUM. The term sternum was originally applied to the whole ventral surface of any thoracic segment and is everywhere used in this sense. This, of course, prohibits the use of the term sternum for a subdivision of itself, although several writers have used it in both senses and thus have allowed opportunity for more or less confusion.

The sternum is probably composed of five subdivisions, which vary greatly in size and shape in different insects. In

some Hymenoptera and Coleoptera they are all fused into one sclerite. Three of these subdivisions are usually present in most insects, while the other two occur in only a few. For these sclerites, I shall use a modification of Crampton's '09, terminology, designating the subdivisions of the sternum as sternites. Thus as far as possible, without leading to confusion, the subdivisions of the tergum, pleuron and sternum will be designated by the endings tergite, pleurite, and sternite respectively.

The presternite (Fig. 4, prs₁), or anterior division of the sternum is derived from the verasternite ("sternum" or "basisternum" of other writers) and is absent in most insects. In the prothorax of *Ectobia lapponica* the presternite is in the process of becoming detached from the verasternite (Fig. 9, prs). In the prothorax of *Capnia* it is completely detached from the verasternite and lies directly in front of it (Fig. 4, prs₁). It is quite a large, oblong sclerite and has frequently been mistaken for one of the neck sclerites, owing to its position. The presternite is also found in the meso- and metathorax of *Capnia* (Fig. 4, prs₂, prs₃) and in the prothorax of *Forficula* (Fig. 8, prs). The presternite is also present in *Raphidia* and has been figured in the metathorax of *Pteronarcys* by Comstock and Kochi, '02. In the latter insect it is similar in shape to the presternite of the prothorax of *Ectobia lapponica* and is attached to the verasternite in the same manner. Comstock and Kochi, '02, have termed it the "presternum." In all other insects examined, the presternite is either absent or indistinguishably fused with the verasternite.

The verasternite is a large sclerite of variable shape lying immediately posterior to the presternite, when the latter is present (Fig. 8, vs₁). It is found in all insects and is often fused at its anterior corners with the precoxale, thereby forming the connecting bridge between the episternum and sternum (Fig. 7, vs₁). In such insects as the Lepidoptera, Diptera, etc., the verasternite is divided longitudinally by a median groove formed by an infolding of the chitin (Fig. 14, vs). Internally this groove is represented by a longitudinal, chitinous ridge. In *Ectobia* the verasternite is divided diagonally by two sutures into four sclerites and the precoxale is not fused with it (Fig. 9, vs).

The furcasternite is situated directly behind the verasternite and is usually a much smaller sclerite, although quite variable in shape in different insects (Fig. 7, fs). It is usually fused with the verasternite, but may be detached as in the prothorax of *Periplaneta* (Fig. 3, fs₁). In insects where fusion of the furca- and verasternite occurs, the former is often divided longitudinally by the median groove, exactly as in the verasternite (Fig. 14, fs). This median infolding of the integument does not occur in primitive insects and is probably a secondary modification of the more specialized forms.

Internally the furcasternite bears two processes or furca. These are usually hollow, strongly chitinized apophyses and are always present (Fig. 3, f). The furcal arms usually abut against the apodemes (pleural arms) and very frequently are closely united with them, thus forming a strong internal connection between the pleuron and sternum.

Externally the furcasternite is easily distinguished, even when fused with the verasternite. Sometimes in such insects as *Capnia*, it is connected with the epimeron (Fig. 4, fs₁). This is brought about by a narrow sclerite (postepimeron), which extends from the epimeron behind the coxa and joins the furcasternite, thus forming a connecting bridge. When the precoxale and verasternite are also fused, a complete ring is formed inclosing the coxa.

The pleural suture, together with the suture which extends between the veracoxa and meron and the one which separates the furca and verasternite, present a condition which has given rise to several double segment theories, but it does not necessarily follow that these sutures mark a division between two segments, as previously discussed.

The furcasternite in the prothorax of *Periplaneta* is a single, transverse, oval sclerite (Fig. 3, fs₁). In the meso- and metathorax it is Y shaped and fused with the verasternite (Fig. 3, fs₂, fs₃). In some forms it is also fused with the spinasternite (discussed later) as in some Lepidoptera, etc., while in others, such as in the prothorax of *Leuctra*, it is divided into two sclerites. Thus there are a few modifications in different insects.

There are indications of a fourth division of the sternum in a few insects, but it is usually absent. In the prothorax of *Capnia*, it is a single, large, oval sclerite, lying behind the

furcasternite (Fig. 4, pfs₁). In *Leuctra* this sclerite is divided longitudinally into two small sclerites. In *Periplaneta* the fourth division or postfurcasternite, is probably represented by two small sclerites on either side of and behind the furcasternite. (Fig. 3, pfs₁).

The spinasternite or fifth division is generally present and usually quite small and variable in shape (Fig. 3, ss). It bears a single internal apophyses, the spina, which is usually hollow. This sclerite lies behind the postfurcasternite, when the latter is present and behind the furcasternite when it is absent. The spinasternite in some insects is free or attached to the mesothoracic verasternite. In others it is either united or fused with the furcasternite. It is so variable in position that it is very hard to tell to which segment the spinasternite belongs, but it probably belongs to the segment in front of it, as no spinasternite has ever been described as occurring in front of the prothoracic verasternite. In the prothorax of *Corydalis*, *Forficula*, etc., it is very small, being represented by the internal apophyses only (Fig. 8, ss₁).

Audouin, '24, applied the term sternum to the entire ventral surface of any thoracic segment. It has since been used to designate various subdivisions of the sternum by different authors and this has naturally led to some confusion.

Mac Leay, '30, thought that each thoracic segment was composed of four subsegments and hence assumed that the sternum was composed of four subdivisions. He accordingly proposed the terms praesternum, sternum, sternellum and poststernellum for these supposed subdivisions.

Newport, '39, adopted Mac Leay's views, but was unable to find four subdivisions in the sternum of any living insect. Mac Leay's terminology, however, has been used by several writers.

Crampton, '09, used the terms presternum, basisternum, furcisternum, postfurcal sclerite and spinasternum, each sclerite being named after some characteristic which it bears. I have adopted this terminology in a slightly modified form, using the prefixes (except "basi") with sternite, to denote the subdivisions of the sternum.

Comstock and Kochi, '02, in their figures of the metathorax of *Pteronarcys* and *Stenopelmatus*, have labeled the first abdominal segment the "sternellum." In their figures of the neck

plates of *Gryllus*, *Periplaneta*, etc., they have designated the posterior ventral cervical sclerite the "sternellum." Consequently it is impossible to decide to what sclerite they intend the term "sternellum" to be applied.

Snodgrass, '09, used Mac Leay's terminology for the sternum, but later he used the term "eusternum" instead of "sternum," to designate the verasternite, or second division of the sternum. Snodgrass, '09, however, found and named only three subdivisions of the sternum, the presternum, sternum and sternellum. The assumed poststernellum of Mac Leay is neither figured nor mentioned. His claim that the presternum consists of two plates and that it is equivalent to the "vorplatten" of German entomologists is incorrect. The presternum consists of only one plate in all insects in which it has been found and the "vorplatten" are parts of the precoxale. Furthermore in his figures, the true presternum is not shown, but in each case some other part of the sternum is designated as the presternum.

Berlese, '06, considered the whole thoracic sternum as composed of the pro-, acro-, meso- and metasternites. He found that each of the latter was divided into two sclerites, which he termed the "sterni" and "sternelli." These subdivisions (sterni and sternelli) are incorrectly homologized in the different insects figured in his work. He has interpreted the "sternelli" as the spinasternite, as the first abdominal segment, as the spinasternite plus the furcasternite, as the verasternite, etc. Hence his interpretations of the sclerites are so inconsistent in his figures, that it is impossible to tell what sclerite he intends to designate by his "sterni" and "sternelli."

INTERSEGMENTALIA. Between the thoracic segments in such insects as the Orthoptera, Plecoptera, Trichoptera, Neuroptera, etc., there are usually a few small sclerites (Fig. 4, i). These vary in number, size and shape in different insects and include the plates surrounding the spiracle when the latter is present. They have been appropriately termed the intersegmentalia (Crampton, '09) because they are situated in the intersegmental membrane.

The intersegmentalia may be either detached portions of the segment in front of them, of the segment behind them, or of both. Which supposition is correct it is impossible to say,

without first working out the musculature of these sclerites. Whether the spiracle belongs to the segment in front, or behind it, is still a disputed question, although it seems very probable that each spiracle belongs to the segment behind it.

In the dorsal neck region of *Periplaneta* there is a small sclerite (Fig. 5, dcs), which seems to be homologous with a similar sclerite found in the dorsal intersegmental region between the pro- and mesothorax of *Corydalis* (Fig. 6, i). This would indicate that the neck sclerites and the intersegmentalia are homologous.

Voss, '04, Heymons, '95, and Palmén, '77, have proposed various theories concerning the spiracles. From a study of the musculature, Voss, '04, claims that they belong to the segment in front of them. From a study of their embryology, Heymons, '95, concluded that they lie in the anterior portion of their respective segments, but may secondarily move forward and become attached to the segment in front of them. Palmén, '77, thought that the first thoracic spiracle might be either pro- or mesothoracic, varying in different insects. It is generally agreed among most workers that the third thoracic spiracle belongs to the first abdominal segment. Of the three theories mentioned, Heymons' seems to have the most support, but more investigation on this point is necessary before it can be definitely settled.

CERVICAL SCLERITES. Embedded in the soft neck region of most insects are found a varying number of sclerites, differing in size and shape in different insects (Fig. 3, lcs, vcs). These sclerites are designated by the term "Cervical Sclerites" (Huxley, '85) or "microthoracic sclerites" (Verhoeff, '02-'04), etc. In this paper the term cervical sclerites will be adopted for these neck plates.

There can be no question that the cervical sclerites of one insect are in general homologous with the cervicals of other insects. But difficulty arises as to the origin of these neck plates and their homologies. They may be either detached portions of the head or of the prothorax or of both, while some have even considered them as the remains of one or more primitive segments. Each of these four theories has its own adherents and which one is correct, it is impossible to say at present. The cervical sclerites furnish support for the head

and it appears very probable that they are detached portions of both the head and prothorax. In some forms such as *Forficula*, *Dolerus*, etc., the lateral cervical bears an inward projecting process (Fig. 14, ap).

In *Periplaneta* there are two large lateral cervicals on either side of the neck and two ventral cervicals (Fig. 3, lcs, vcs). The lateral sclerites articulate with the head and prothoracic precoxale. This is true of all insects where the lateral cervicals occur except when they are fused with the precoxale and episternum (Fig. 7, lcs). In the latter case they articulate with the head alone (Fig. 12, lcs). The lateral cervical sclerites in *Periplaneta* articulate with small sclerites attached to the head as shown in (Fig. 3, a). The lateral cervicals very nearly meet in front of the prothoracic verasternite in *Periplaneta* (Fig. 3, lcs). The lateral cervical sclerites in *Gryllus* consist of one large plate on either side of the neck, which probably represents the fusion product of the two lateral sclerites found in the roach and other insects (Fig. 7, lcs). The two ventral sclerites in the roach, have evidently become split into five small sclerites in *Gryllus* (Fig. 7, vcs).

There is only one ventral cervical sclerite in *Forficula* and *Capnia*, the other having disappeared, while the lateral cervicals in the former are more numerous than in the latter (Figs. 8 and 4). Both of these insects have a large, more or less oval sclerite situated directly in front of the prothoracic verasternite (Figs. 8 and 4, prs), which has been mistaken by several writers for a cervical sclerite. This sclerite is in reality the presternite, which has become detached from the verasternite. In the prothorax of the roach *Ectobia lapponica*, the presternite is seen in the process of becoming detached (Fig. 9, prs). It has been found, however, in only a few insects.

The cervical sclerites are quite numerous in the lower insects such as *Periplaneta*, *Gryllus*, etc. (Figs. 3 and 7). In the higher insects (Neuroptera, Lepidoptera, Diptera, etc.), there is a tendency for the cervical sclerites to fuse together and increase in size, which becomes more marked in the more specialized forms (Fig. 2, lcs). The cervical sclerites in many Coleoptera have disappeared or have become indistinguishably fused with the prothoracic plates. In some Hymenoptera (Tenthredinidæ) the lateral cervicals have become fused with the prothoracic episternum (Fig. 12, lcs).

Snodgrass, '10, from a study of the Hymenopteron thorax, concluded that the large sclerite which lies in front of the coxa and "prosternum" (prothoracic verasternite) of sawflies, was the "proepisternum" (Fig. 15, lcs). He bases his claim upon the position of the pleural suture. A small sclerite which adjoins the "proepisternum" dorsally in *Dolerus*, he admits is a cervical sclerite (Fig. 12, lcs). The conclusions reached by Snodgrass, '10, appear incorrect for several reasons. It is more probable that the conditions found in the prothorax of sawflies, is the result of a fusion of the cervical sclerites with the episternum, in which the cervicals have become enlarged and the episternum and epimeron have become greatly reduced in size. The fusion and enlargement of the cervicals is very noticeable in the higher insects (Tipulidæ) while a reduction of the episternum and epimeron is found in practically all insects. Furthermore, the episternum never meets in front of the prothoracic verasternite and never articulates with the head, as do the cervical sclerites and also the "proepisternum" of Snodgrass, '10, in the sawflies.

A more conclusive proof that sawflies have a large lateral cervical may be obtained from a study of *Abia*, *Dolerus*, and *Macroxyela* in the order named. In the prothorax of *Abia* the precoxale or bridge which connects the episternum with the verasternite in a large number of insects can be plainly seen (Fig. 15, pc). It extends from the coxal process to the verasternite, thereby connecting the episternum and verasternite. The episternum has never been known to occur in front of the precoxale, but the cervical sclerites are always situated anterior to it. The large sclerite which lies in front of the coxa and the "proepisternum," also lies in front of the precoxale. Hence this sclerite cannot be the prothoracic episternum, or "proepisternum," but must be a lateral cervical sclerite. In *Dolerus* the precoxale is in the process of disappearing (Fig. 12, pc). It is represented on either side of the prothoracic verasternite by a small sclerite (Fig. 12, pc), while in *Macroxyela* it has entirely disappeared (Fig. 14). In the latter insect however, the verasternite has greatly increased in size and may possibly represent the fusion product of the verasternite and part of the precoxale (Fig. 14, vs). A cleft indicating a possible splitting of the lateral cervical is seen in *Macroxyela* (Fig. 14). The episternum and epimeron are clearly marked off by sutures in the prothorax

of *Dolerus* and are seen to be much reduced in size (Fig. 12, es, em₁). From the above facts, it seems very probable that the large sclerite in sawflies, which Snodgrass, '10, calls the "proepisternum," is really a large lateral cervical sclerite, fused with the episternum and in some cases with the epimeron also. The fact that an internal process is present at the point of articulation of the "proepisternum" with the head (Fig. 15, ap), signifies that this plate is a cervical sclerite, since a similar process is found on the lateral cervicals of several other insects as in *Gryllus*, *Forficula*, etc.

When the epimeron is absent in the prothorax of sawflies, Snodgrass, '10, considers the internal process or pleural arm, as apparently not the homologue of the pleural arm of the other segments, since it does not arise between the plates (Fig. 14, pla). This may be true, but in all cases the pleural arm is joined to the furca of the furcasternite as in other segments and in other insects. If the epimeron has apparently disappeared in the prothorax of some sawflies, it may be represented by a part of the pleural arm itself, especially if it be true that the pleural arm is formed by an infolding of the integument. Thus it would seem more probable that the pleural arm in the prothorax of sawflies, in which the epimeron is absent, is the homologue of the pleural arm of other segments and of other insects.

Several theories have been formulated to account for the origin of the cervical sclerites.

Straus-Durckheim, '28, suggested that the cervical sclerites represent the remains of two segments, situated originally between the head and prothorax. He designated them by the term "pieces jugulaire."

Newport, '39, considered them as detached portions of the prothorax and called them the prothoracic "paraptera."

Lowne, '70, regarded the cervicals as a part of the labial segment or last cephalic segment of the head. This theory was later adopted and supported by Huxley, '85, Comstock, '02, Riley, '04 and others. Although Riley, '04, regards the lateral cervical sclerites as the pleurites of the labial segment of the head, he also states that part of the pleural region of the labial segment is already included in the head capsule. Lowne, '70, applied the terms "condyle" to the lateral cervicals and

"cephlo-sternum" to the ventral cervicals. Huxley, '85, used the term cervical sclerites to designate the neck plates.

Lowne, '90, considered the cervicals as detached portions of the prothorax, thereby accepting the theory formerly proposed by Newport, '39.

Verhoeff, '02-'04, adopted and elaborated the theory advanced by Straus-Durckheim, '28, viz., that the cervicals represent two segments originally situated between the head and prothorax. He termed the neck region the "microthorax" and designated the various sclerites by the terms, "coxopleure," "anapleure," etc. This theory was severely criticized by Silvestri, '02, Börner, '03, Voss, '04, Desguin, '08, and others. They proved conclusively that Verhoeff's "microthoracic" theory was unsupported by anatomy, embryology, musculature, etc.

Berlese, '06, regarded the cervical sclerites as belonging to the head and prothorax.

Snodgrass, '08, adopted Verhoeff's theory of the "microthorax," but later Snodgrass, '09, repudiates the "microthoracic" theory, adopting the term "cervicum" of Crampton, '09, for the neck region.

SUMMARY.

The thorax is composed of three segments, the pro-, meso-, and metathorax.

All compound segment theories are not based upon enough facts to be acceptable at present.

The thorax of primitive insects, larvae, etc., is composed of numerous small sclerites, which become fused to form the sclerites of the higher insects.

A secondary fusion or a splitting of sclerites often occurs. Certain specialized forms often retain some characters of primitive insects.

The tergum of winged insects is composed of two sclerites, which are usually subdivided into regions.

The wing articulates with two processes on the lateral margin of the tergum and with the alar plates at the base of the wing. Ventrally it articulates with the pleural wing process.

The pleuron is represented by a single sclerite in some primitive insects. (*Eosentomon*).

The pleural suture is always present, together with the apodeme, and they are probably formed by the infolding of the integument due to muscular stress or similar causes.

The pleuron may be connected dorsally with the tergum at its anterior and posterior end by a bridge and ventrally with the sternum in a similar manner.

The episternum and epimeron are subdivided into an upper and lower region in some insects. (*Mantispa*).

The sternum is composed of five subdivisions in a few insects. (*Capnia*, *Ectobia*, etc.)

The presternite is present as a large, oval sclerite, lying in front of the prothoracic verasternite in *Capnia* and *Forficula*. It is considered as a large ventral cervical by most writers.

The large sclerite which lies in front of the coxa in the prothorax of sawflies, is largely composed of the lateral cervical, fused with the episternum, and in some cases with the epimeron also.

The cervical sclerites are detached portions of the head and prothorax and are homologous with the intersegmentalia, which are probably derived from the segments directly anterior and posterior to them.

In some insects the coxa is composed of two parts, the meron or posterior portion and the veracoxa or anterior portion. The meron is part of the coxa and derived from it.

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TERMINOLOGY.

The sub-figures 1, 2, and 3 indicate that the sclerites belong to the pro-, meso- and metathorax respectively.

- a—sclerite attached to base of head in *Periplaneta*.
 aba—anterior basalar.
 ac—antecoxale.
 ad—apodeme.
 ap—apophysis.
 atn—antetrochantin.
 ba—basalar sclerites.
 cm—coximarginal sclerite.
 cs—cervical sclerite.
 cx—coxa.
 exp—coxal process.
 des—dorsal cervical sclerite.
 el—elytra.
 em—epimeron.
 es—episternum.
 esp—anepisternum.
 f—furca.
 fs—furcasternite.
 g—suture dividing episternum into two regions.
 h—halteres.
 i—intersegmentalia.
 inplt—inner pleurotergite.
 iplt—inferior pleurotergite.
 kem—katepimeron.
 lcs—lateral cervical sclerite.
 m—meron.
 mp—meropleurite.
 msn—mesonotum.
 msst—mesosternum.
 mt—mediotergite.
 mtu—metanotum.
 mtst—metasternum.
 o—suture dividing episternum and precoxale in *Periplaneta*.
 oplt—outer pleurotergite.
 pba—posterior basalar sclerite.
 pc—precoxale.
 pem—postepimeron.
 pes—pre-episternum.
 pfs—postfurcasternite.
 pla—pleural arm.
 ple—pleurocoxale.
 pls—pleural suture.
 plt—pleurotergite.
 pltn—pleurotrochantin.
 plwp—pleural wing process.
 pn—pronotum.
 prs—presternite.
 prsc—prescutum.
 psl—postscutellum.
 ptu—post-trochantin.
 ptp—pteropterite.
 sa—subalar sclerite.
 sc—scutum.
 scsl—scutoscutellum.
 sl—scutellum.
 sp—spiracle.
 spa—abdominal spiracle.
 spplt—superior pleurotergite.
 ss—spinasternite.
 stc—sternocoxale.
 stp—sternopleurite.
 tm—tergum.
 tn—trochantin.
 tnl—trochantinelle.
 tnm—trochantin major.
 vcs—ventral cervical sclerites.
 vex—veracoxa.
 vs—verasternite.
 w—wings.
 1st a—1st abdominal segment.

EXPLANATION OF PLATES.

Owing to the nature of the thorax, the figures are necessarily somewhat diagrammatic, but as far as possible, represent the natural condition of the sclerites as they occur in the thorax of these insects. In lateral views the anterior end faces the right side of the page. In ventral and dorsal views the anterior end faces the top of the page.

PLATE I.

- Fig. 1. A lateral view of the thorax of *Tipula*, including part of the dorsum and the first abdominal segment. Head, wing and the greater part of each leg removed.
- Fig. 2. A lateral view of the thorax of *Leptis*, including part of the dorsum and the first abdominal segment. Head, wing and the greater part of each leg removed.

PLATE II.

- Fig. 3. A three-quarters view of the thorax of *Periplaneta*, showing the ventral and lateral sclerites, together with the edge of the pronotum and wings. Head and the greater part of each leg removed.
- Fig. 4. A three-quarters view of the thorax of *Capnia*, showing the ventral and lateral sclerites, together with the edge of the pronotum and wings. Head and the greater part of each leg removed.
- Fig. 5. Dorsal cervical sclerites of *Periplaneta*.
- Fig. 6. Dorsal intersegmentalia, occurring between the pro- and mesothorax of *Corydalis*.

PLATE III.

- Fig. 7. A three-quarters view of the thorax of *Gryllus* including the lateral and ventral sclerites, together with the edge of the pronotum and wings. Head and greater part of each leg removed.
- Fig. 8. A three-quarters view of the thorax of *Forficula*, including the lateral and ventral sclerites and the edge of the pronotum and wings. Head and greater part of each leg removed.
- Fig. 9. A three-quarters view of the prothorax of *Ectobia lapponica*, including the ventral and lateral sclerites, and the edge of the pronotum. Head and greater part of each leg removed.
- Fig. 10. A lateral view of the mesothorax of *Corydalis*, including part of the tergum and sternum. Most of the leg removed.

PLATE IV.

- Fig. 11. A lateral view of the thorax of *Tabanus*, including part of the dorsum. Head, wing and the greater part of each leg removed.
- Fig. 12. Ventral view of the prothorax of *Dolerus*, showing ventral and lateral sclerites. Head and greater part of each leg removed.
- Fig. 13. Lateral view of the thorax of *Chrysopa* including part of dorsum and first abdominal segment. Head, wing and greater part of each leg removed.
- Fig. 14. A ventral view of the prothorax of *Macroxyela*, showing ventral and lateral sclerites. Head and most of each leg removed.
- Fig. 15. Ventral view of the prothorax of *Abia*, showing ventral and lateral sclerites. Head and most of each leg removed.